THE OHIO JOURNAL OF SCIENCE

PUBLISHED BY THE

OHIO STATE UNIVERSITY SCIENTIFIC SOCIETY

VOLUME XVII DECEMBER, 1916 No. 2

TABLE OF CONTENTS

THE RELATION OF THE PROFUNDUS AND GASSERIAN GANGLIA IN THE EMBRYO OF THE URODELE, PLETHODON GLUTINOSUS.

KATHERINE W. OKEY,
Department of Anatomy, Ohio State University.

INTRODUCTION.

In such lower fishes as the Selachians both a profundus and a Gasserian ganglion are present as separate ganglia in the adult form. Many ganoids and all teleosts, with the single recorded exception of Trigla, show modifications of the condition in Selachians, by the apparent loss of the profundus ganglion or by its fusion with the Gasserian in the adult. (Allis. '97). Likewise in every adult form of Amphibia so far described the Gasserian is the only ganglion on the trigeminus nerve. No separate profundus ganglion is present, although rami from the Gasserian ganglion are homologized with all or portions of the ramus opthalmicus profundus found in Selachians.

The assumption has been made that the profundus ganglion has in the Amphibia fused with the Gasserian to form what Coghill ('02) calls "a fused ganglionic complex" in which rami representing both of the ganglionic components have their origin. Evidence for the proof of this specific assumption is wanting, although in the study of Rana embryos by Landacre and McClellan ('12) and of a Plethedon embryo by Kostir in an unpublished paper summarized in Fig. 29, it was found that certain ganglia, other than these two, which form complexes in the adult stand out separate and distinct in the embryo.

The results of these studies of embryonic conditions indicate a process of fusion in the ontogenetic development of certain ganglionic complexes other than that of the trigeminus. As stated above, it has been assumed that fusion takes place in the phylogenetic development of the profundus and Gasserian ganglia. So far as I know, however, the ontogenetic development of these two ganglia has not been studied in a form where they are separate in the embryo and form one complex in the adult.

The profundus ganglion has been found separate from the Gasserian in an early embryo of Lepidosteus, (Landacre '11) and distinct but not detached from the Gasserian in Rana (Landacre '12) and in the 11.5 mm. embryo of Plethedon glutinosus referred to above, but the exact relations of the profundus and Gasserian in the ontogeny of a favorable form have not been followed in detail. The present study was, therefore, undertaken with the purpose of determining the exact relations of the profundus and Gasserian ganglia in the early ontogeny of a typical urodele amphibian, Plethedon glutinosus.

This study was preceded by that of Kostir in an unpublished work on the 11.5 mm. embryo of Plethedon gl. and is an endeavor to trace the profundus and Gasserian ganglia from the condition in this 11.5 mm. embryo to earlier stages where the ganglia are separate and to describe their exact relation at critical stages.

This problem has definite limitations and no final conclusions concerning the phylogenetic relations of these two ganglia can be drawn from the results of this study, but if similar studies were made on a sufficient number of types in the vertebrate series, light would undoubtedly be thrown on the fate of the profundus and Gasserian in phylogeny.

I wish to express my gratitude to Professor Landacre for the help, constant encouragement and inspiration he has given me during the progress of this study.

Material and Methods.

The material used consists of a series of embryos of Plethedon taken from four lots of eggs collected at the same time. There are thirty-eight stages taken at intervals of from 3½ to 7½ hours, or an average of 4 hours. These range in length from 6 mm. to 11.5 mm. All were killed and fixed in Zenker's fluid, cut in transverse sections 10 micra thick and stained with Daelafield's hæmetoxylin and orange G.

No 30 of this series closely corresponds to the 11.5 mm. embryo studied by Kostir. Of the present series three stages were chosen for detailed study. These are:

Series:

M.—9 mm. in length.
G.—7 mm. in length and 26½ hours younger than M.
B.—6 mm. in length and 28½ hours younger than G.

Three flat reconstructions at a magnification of 150 diameters, detailed drawings at magnification of 520 diameters, and outlines at magnification of 80 diameters were made of the selected stages with the aid of a camera lucida.

The methods of study were in brief as follows:

After an examination of all 38 stages of the series, three stages as mentioned above, uniform in fixation and staining and exactness of transverse section, were selected as representing the most critical phases in the progressive development of the ganglia in question. The method of reading from later to younger stages was observed and the descriptions of the specific stages are given in this order. The histological characteristics of the ganglia were determined in the later stages since recognition of the ganglia at younger stages depends on a knowledge of the distinguishing features of their nuclei and cytoplasm, as well as of their position.

In the selection of sections for detailed drawing, care was taken to choose, when possible, comparable levels from the different stages in order to make simpler the comparison of the ganglia at different stages.

The aim was to choose from each stage one section: (a) near the anterior end of profundus; (b) at the level of the optic stalks; (c) through the roots of the ganglion; (d) through the main portion of the Gasserian, and any other sections necessary to make clear the description.

In the course of the study a count was made of the nuclei in the ganglia at each stage. In making this count the principle was adhered to of counting every nucleus visible in cross section. Many nuclei were thus recounted, but the error is apparently constant for all stages and would not effect the ratio in the results.

General Features.

The profundus and Gasserian ganglia which together form the trigeminus complex lie in front of the auditory vesicle and are the most anterior of all the pre-auditory ganglia in this form, except the ganglion of the nervus terminalis. Their general position is anterior to the facial ganglia and the auditory vesicle and in the region of the optic vesicle.

The profundus may, however, extend as far anterior as the region of the nasal capsule and the Gasserian as far posterior as the first visceral pouch of the pharyngeal region.

The ganglia are usually more or less completely surrounded by the loose mesenchyme, which fills the head region. The mesenchyme cells have rather large, light staining nuclei and unpigmented cytoplasm containing very large yolk granules and seems to be composed of mesentoderm. The cells of the ganglia have the opposite characters of small, darkly staining nuclei, like the ectoderm and small, obscure yolk granules.

This contrast in histological character makes it possible to determine the limits of the ganglia and the mesenchyme at any stage.

Description of the 9 mm. stage.

In the 11.5 embryo of Plethedon gl. described by Kostir, the Gasserian ganglion (Fig. 29, Gass. G.) is a large mass, oblong in cross section lying wedged between the brain and the optic vesicle. The anterior end of the profundus portion extends for some distance forward between the brain and the optic vesicle. From the ganglionic complex arise three nerve trunks: (a) The opthalmicus V from the anterior end; (b) the maxillaris V, and (c) the mandibularis V which fork over the temporalis and masseter muscles.

The trigeminus ganglion is attached to the medulla by a fibrous root, long antero-posteriorly. The nuclei of the ganglia have the usual dark staining properties and at this stage are very closely packed together.

The 9 mm. embryo (Fig. 30 and Fig. 1-6) is the oldest stage of my series. It shows a fused condition of the profundus and Gasserian ganglia and at the root it is impossible to distinguish between the two portions of the ganglionic complex.

At the anterior end, anterior to the level of the optic stalks, the profundus ganglion consists of a small mass of pigmented cells dorso-mesial to the optic vesicle and in contact with it (Fig. 2 and 3 Prof. G). At the level of the optic stalks the profundus is a larger oval and compact mass (Fig. 3, Prof. G), in about the same position as in the more anterior sections. At a point about one-half of the total length of the ganglion from the anterior end, the ganglion becomes larger and round in cross section, and lies mesially towards the ventro-lateral border of the medulla. Just posterior to the optic vesicle the profundus and Gasserian ganglia are joined and attached by a fibrous root to the medulla at its ventro-lateral border. In these sections the first visceral pouch of the pharynx is beginning to appear as an evagination of the endoderm (Fig. 5, Ph. P. I) accompanied by condensation of mesenchyme.

Posterior to the root of the ganglionic mass the Gasserian portion forks over the first visceral pouch in about the position where the maxillary V and mandibular V nerve trunks arise in later stages (Fig. 6, Gass G.). These trunks are entirely cellular at this stage. Near its posterior end the Gasserian ganglion becomes loose in texture. The dorsal lateralis ganglion on VII appears dorso-lateral to the Gasserian in the most posterior sections of the Gasserian. (Fig. 6, D. L. VII). No histological differences between the two ganglia are apparent at this stage (9 mm.) although in the 11.5 mm. stage the nuclei of cells of the lateral line ganglia are larger and lighter staining.

Description of the 7 mm. Stage.

At this stage the profundus ganglion is very large and more prominent than the Gasserian. It is in contact with the Gasserian at its proximal end, but enters the medulla by a separate root. The profundus projects anteriorly from its point of contact with the Gasserian and lies dorsal to the optic vesicle. The Gasserian consists of a mass in contact with the medulla and of a ventro-lateral projection. The dorsal lateralis ganglion on VII lies lateral to the distal part of this extension. The general relations are shown in the flat reconstruction. (Fig. 31).

The extreme anterior end of the profundus ganglion lies between the ectoderm and the fore brain dorsal to the anterior end of the optic vesicle. Figure 7, (Prof. G.) shows the character of the ganglion near its anterior end. It is a small, ragged mass of pigmented cytoplasm containing nuclei of moderate size and dark staining properties. Mesially and ventrally it is in contact with mesenchyme and laterally it is separated from the ectoderm by a thin layer of mesenchyme, in which some darkly staining nuclei appear.

An interesting feature observable in this figure (Fig. 7) is the relation of the profundus ganglion (Prof. G) to the large ectodermal thickening (Pl.) lateral to it. This thickening is a placode, which farther posterior shows more noticeably the radial arrangement of cells characteristic of the lateral line organs and is identified as a supra-orbital lateral line placode. This placode is apparently formed by proliferation of cells in both layers of ectoderm. The cells of the outer non-nervous layer have no definite arrangement but those of the inner nervous layer lie with their long axes at right angles to the surface. Cell boundaries may sometimes be clearly made out in the placode. Mitotic figures such as seen in Figure 7 (Pl.) are numerous in the placode. Both of these facts are in contrast to the condition in the profundus ganglion. (Prof. G.).

Posterior to the level of figure 7 the ganglion becomes rounder and more compact and definite. Posterior to the optic stalks it lies slightly farther from the ectoderm. Figure 9 (Prof. G) shows a transverse section of the ganglion at the point of evagination of the optic stalks and the middle of the crystalline lens invagination. (C. L.)

At this level (Fig. 9) the profundus ganglion lies, as before, (Fig. 7) very near the supra-orbital lateral line placode. The boundaries of the ganglion are clean cut and its limits are readily distinguishable from the surrounding mesenchyme (Fig. 10, Prof. G). The nuclei seem to vary a good deal in size.

From a point posterior to the level shown in figure 9, to its root in the medulla the profundus ganglion appears to move mesially. It retains its compactness, but is smaller in transverse section than in preceding sections. Gradually it becomes looser in structure and shows a mesial projection until at the level of Figure 11, the profundus is attached to the ventro-lateral region of the medulla by a small, necklike cellular root (Rt. Prof. G). It is noticeable that the boundaries of the profundus at this level are uneven and irregular. The outline (Fig. 12) shows that the supra-orbital lateral line placode (Pl.) persists at this level, which is near the posterior end of the optic vesicle (O. V.).

Immediately posterior to the beginning of the root of the profundus the Gasserian ganglion increases in size and 10 micra posterior to the level of figure 12 it comes to lie in contact with the profundus. The profundus forms the dorso-mesial portion of the ganglionic mass and the Gasserian the ventro-lateral portion. Just posterior to this first contact with the profundus the Gasserian enters the medulla by a large, cellular root. (Fig. 13 Rt. Gass. G.)

The Gasserian portion remaining consists of a small, triangular mass in contact with the medulla and a larger rectangular mass extending ventro-laterally to the region of the first visceral pouch. As one reads posteriorly the ganglionic mass dorsal to the gill pouch increases in size and comes to lie as an irregular oblong near the supra-orbital placode and dorso-lateral to the first gill pouch. It is connected by a narrow neck with the proximal portion. The neck portion then drops out, leaving the condition shown in Figures 15-16, where the two parts of the ganglion are entirely separate. Only the larger portion (Fig. 15, Gass. G.) is figured in detail. Its close relation with the first visceral pouch (Ph. P. I) is shown in the outline (Fig. 16) while the detail drawing (Fig. 15) shows its slight lateral contact with the supra-orbital lateral line placode (Pl). At its ventro-lateral border the ganglion is irregular in outline and is at one point in close contact with the ectoderm just ventral to the placode. At its extreme ventro-lateral edge the ganglion comes into contact with the ectoderm of the first visceral pouch (Ph. P. I).

Slightly posterior to this level the proximal portion of the Gasserian drops out, leaving only the part over the gill pocket. At this same level a few nuclei of the dorsal lateralis ganglion on VII appear as a loose mass dorso-lateral to the Gasserian (not figured). The dorsal lateralis ganglion of VII is very near the ectoderm and dorsal to the gill pouch. It retains this position for several sections. The Gasserian becomes gradually smaller and more vaguely marked out and drops out just posterior to Fig. 15.

Description of the 6 mm. stage.

The profundus ganglion is in the 6 mm. stage a loose mass extending for about one-fifth its length anterior to the optic vesicle and for four-fifths of its length is in contact with the lateral ectoderm. The Gasserian at this stage is hard to define. It has no root entering the medulla, but lies close to it. A ventro-lateral extension projects to the region of the first visceral pouch. At this stage the Gasserian and the profundus are isolated from one another by a distance of three-eighths the length of profundus, as may be seen in the flat reconstruction of this stage. (Fig. 32).

The anterior end of the profundus ganglion lies in the region of the fore brain just anterior to the optic vesicle. Near its anterior end it consists of a loose mass of pigmented cells attached to the ectoderm (Fig. 17, Prof. G.).

The anterior portion of the ganglion lies in contact with the ectoderm throughout most of its dorso-ventral diameter. The greater part of this contact is immediately anterior to the supra-orbital lateral line placode. This contact continues to a point just anterior to the crystalline lens invagination. Posterior to its loss of connection with the ectoderm the profundus becomes very indefinite. There are only a few nuclei and these are separated from each other by cytoplasm and yolk granules (Fig. 21). The profundus retains its position dorsal to the optic vesicle until it drops out. At the level of the open optic stalks no trace of a ganglionic mass is found. None appears until the level of the anterior end of the Gasserian. (Fig. 23-24 and Fig. 32, Sec. 76). This mass consists of a few ganglion cells lying between the medulla and the ectoderm just posterior to the open optic stalks (Fig. 24, Gass. G.). In this group the ganglion cells have many cytoplasmic processes and large yolk granules are mingled with them. For the next ten or more sections the Gasserian ganglion is an irregular triangular mass with its base in contact with the lateral part of the medulla and its apex extending ventro-laterally to the region of the first gill pouch.

At the level of figure 25 and figure 32 the Gasserian (Gass. G.) is diffuse and has many strands of cytoplasm running parallel to the long axis of the ganglion. A few sections posterior to this point the Gasserian has two nucleated portions, one a small triangular part near the medulla and the other a large distal part lying over the gill pocket, as in the 7 mm. stage. These two portions are connected by pigmented cytoplasm.

At the level of figure 27, Plate IV, almost at the posterior end of the optic vesicle the Gasserian is restricted to a few cells over the first gill pouch. The supra-orbital lateral line placode (Pl) is large and shows a radial arrangement of cells. For a few sections posterior to Figure 27, the cells of the Gasserian are mingled with the ectoderm at the apex of the first gill pouch. They are apparently continuous with the inner layer of the ectoderm lateral to the endodermal pouch.

The Fusion of the Profundus and Gasserian Ganglia.

The form relations of the profundus and Gasserian ganglia in the specific stages described above furnish abundant evidence for the fusion intact of these ganglia. However, in order to determine whether there is other evidence bearing on this question aside from that of form relation, a count of the nuclei in the ganglia was made according to the principle stated on page 27.

Table 1. Showing the number of nuclei in the profundus and Gasserian ganglia before and after fusion.

Stage	*Length*	*No. of Nuclei*
B	6 mm.	Gass. 480, Prof. 570.
G	7 mm.	Trigeminal Complex 1330
M	9 mm.	Trigeminal Complex 1350.

In the 6 mm. stage the Gasserian has only 480 nuclei, at 9 mm. the trigeminal complex has 1350. It is obvious that this increase in number of nuclei is due mainly to the fusion of the profundus portion with the Gasserian. The number of nuclei in the trigeminal complex in the 9 mm. stage is a little more than the sum of the number of nuclei in the gasserian and profundus at the earlier stage where the two ganglia are separate.

The increase in number of nuclei from 1050, the sum of the nuclei of profundus and Gasserian in the 6 mm. stage before fusion, to 1350 in the 9 mm. stage may be partly accounted for by mitosis. Although the mitotic figures in the ganglia at any stage are extremely scarce, the maximum is 10 in the ganglion at any one stage. The difference is 200 nuclei. At the maximum rate of 10 for every stage between 6 mm. and the 9 mm.

stage, i. e., for 12 stages, the increase by mitosis during this period would be 120 nuclei. This leaves a margin of 80 nuclei for error and possible increase in rate of growth during the stages.

This count of the nuclei seems to fully confirm the other evidence for the fusion intact of the ganglia in question and leave no doubt of its certainty.

The question, however, of the possible disintegration of the Profundus portion in later stages where its identity is in part lost deserves attention. The evidence for disintegration is slight for the boundaries of profundus becomes more and more definite from early stages up to the time of fusion and there is slight evidence of shelling off of cells into the mesenchyme.

If the profundus disintegrated one would expect to find an increasing looseness in the mass and increasing difficulty in determining its boundaries up to the time of fusion. So far as I have observed the opposite is true, during its development. The profundus never behaves as a disintegrating structure, but in fact always contains some mitotic figures which are proofs of continued growth. The comparative rate of growth of the Gasserian and profundus through all stages in their development has not been determined, but the comparative rate at the selected stages furnishes significant proof that the profundus is not breaking down.

In the 6 mm. stage there is one figure in profundus and there are two in Gasserian. The rate of growth is slow for both ganglia at this stage, which is soon after their formation, and for several series the chief characterisitc of their behavior is the aggregation of cells. In the 7 mm. stage there are 10 figures in the two ganglia combined and seven of these are in the profundus. This is a period of comparatively rapid growth and the rate of growth is much higher in the profundus than in the Gasserian. The profundus is evidently the more active of the two ganglia. In the 9 mm. stage there are only four figures in the ganglionic complex. This is the beginning of a period of differentiation and of the formation of fibrous roots and nerve trunks and is marked by a slowing up in the growth process. Even at this stage, however, the profundus is as active as the Gasserian.

Aside from the facts just cited there are other evidences of the persistence in the trigeminal complex of the profundus.

(1) It forms a root which enters the medulla and during development this root shows no signs of disintegration. (2) Although the ganglionic mass is at every stage a syncytium in which the cell boundaries are not easily discerned, there is no indication of the breaking down of nuclear material at any stage. This, if present, might indicate disintegration. The nuclear boundaries become, in fact, more definite from early to late stages.

Summary of the Relations of the Profundus and Gasserian Ganglia From the 6 mm. Stage to the 11.5 mm. Stage.

A comparison of the flat reconstructions of the selected stages of the development of the profundus and Gasserian ganglia makes evident the following points: (Figs. 29, 30, 31, and 32).

(1) The anterior end of the profundus ganglion shifts from early to late stages. It moves from a point at the anterior end of the optic vesicle (Fig. 32) where it is in contact with the lateral ectoderm to a position mesial to the optic vesicle at a level half way between the optic stalks and the anterior end of the vesicle (Fig. 29). In this position it has of course no contact with the lateral ectoderm.

(2) Roots appear in the 7 mm. stage (Fig. 30) as development proceeds and there is a slight shifting ventrally of the roots from the position in earlier stages.

(3) There is a change in the shape of profundus from an irregular oval mass over half as long as broad at its widest point and tapering at both ends in early stages to an elongated tongue-like projection, broad at the proximal and narrow at the distal end in later stages. The level of the greatest dorso-ventral breadth of profundus moves progressively posterior with reference to the position of the proximal end of the Gasserian. (Fig. 29-32).

(4) There is a change in the form of the ventro-lateral projections of the Gasserian ganglion from younger to older stages. It changes from a single large, rectangular projection extending to the first visceral pouch to a comparatively slender projection forked over the temporalis muscle.

(5) There is an absence of the close relation with D. Lat. Gang. on VII in the younger stages which is present in the older stages.

A comparison of comparable levels of the specific stages described, for instance, a comparison of the section at the level of the optic stalks in the 7 mm. stage with the section at about the same level in the 9 mm. stage, confirms the general features observable from flat reconstructions and in addition shows the following characteristics:

(1) Both Gasserian and profundus increase markedly in compactness and definiteness of boundary from early to late stages. The proportion of cytoplasm to nuclei appears to decrease.

(2) Mitotic figures or other evidence of growth by this method are rare in both ganglia at any stage, although they are numerous in surrounding structures.

(3) The ganglion cells can always be distinguished from those of the surrounding mesenchyme because of their pigmented cytoplasm and small yolk granules, and small, quite uniformly darkly staining nuclei. In the youngest stage large yolk granules are sometimes seen in the ganglion, but in the older stages there seems to be no evidence of the mingling of the mesenchyme with either ganglionic mass, i. e., either profundus or Gasserian, nor of the shelling off of ganglionic cells into the surrounding mesenchyme.

(4) The anterior end of profundus in the 6 mm. and the 7 mm. stages lies close to a supra-orbital placode.

(5) The ventro-lateral projection of the Gasserian is closely associated with the first visceral pouch.

The relation of the anterior part of profundus to the supra-orbital placode is a very striking one. Until however the origin of the profundus ganglion and of the lateral line system have been described for this type, one is not justified in attempting to explain the significance of this relation. The same may be said for the relation of the ventro-lateral extension of the Gasserian ganglion to the first visceral pouch.

The Phylogenetic Relations of the Ramus Opthalmicus Profundus.

In order to make clear the bearings of the results of this ontogenetic study on the phylogenetic history of the profundus, it will be necessary to summarize the relations of the profundus ganglion and its nerves in the vertebrate phylogenetic series. Table 2 is a synopsis of the conditions in great part as given by Allis '97.

TABLE II—Showing the Phylogenetic Relations of the Profundus Ganglion and its Nerve Trunks.

Phylum—Chordata (In part after Allis, '97.)
Class—Pisces
Sub Class—Elasmobranchii
Order—Selachii

Genus	*Prof. G.*	*Rt. Prof. G.*	*Rami Prof.*	*Innervation*
Laemargus (Ewart '89, '96) (See Allis '97, p. 535)	Separate from trigeminus in adult.	Fairly separate from trigeminus some communicating branches.	(1) r. op. prof. which divides into (a) small branch above rectus superior muscle, (b) main branch under rectus internus.	Cutaneous and subcutaneous tissue of the snout.
Raja (Ewart '89) (See Allis '97, p. 535-6)	Separate from trigeminus in adult.	Root more intimately connected with root of trigeminus.	r. op. prof. below superior and inferior recti and obliquus, superior; below trochlaris and superior branch of oculomotor. (Schwalbe '79) (See Allis, p. 537).	
Torpedo (Ewart '90)	Separate from trigeminus in adult.			
Acanthias vul. (Mitrophanow by Allis) (See Allis '97, p. 537)	Mesocephalic ganglion, (homologized with the profundus ganglion of Amia) separate from trigeminus in the embryo.	A prolongation of the posterior root of the trigeminus.	r. op. prof. porto prof.	
Sub Class—Ganoidii *Genus* Amia (Allis '97) pp. 593, 532.	Separate ganglion in adult.	Separate in 12 mm.embryo but somewhat fused in adult.	A large portio op. prof. which runs above all the muscles of the eye and joins op. sup. V several ciliary nerves and a small degenerating r. op. prof. from ganglion between dorsal and ventral angle.	

TABLE II—Continued.

Genus	*Prof. G.*	*Rt. Prof. G.*	*Rami Prof.*	*Innervation*
Lepidosteus (Schneider) (See Allis '97, p. 540) (Landacre '12)	Separate ganglion in adult.		10 mm. embryo. R. op. prof. from anterior end of Prof. G. dorsal to optic vesicle Associated with R. O. S. VII (Landacre '12, Fig. 1). *Adult.*—portio op. prof. probably No. r. op. prof.	
Sub Class—Teleostomi				
Menidia (Herrick '99) (pp. 362-66)	Not isolated in adult. A portion of Gasserian ganglion isolated and fused with most cephalic ganglion of sym. system.	Fused with root of trigeminus.	Portion of cutaneous fibres from isolated Gasserian ganglion, which are fused with radix longa of ciliary ganglion tentatively homologized with r. op. prof. No. portio op. prof.	
Trigla (Stannius '49) (See Allis '97, p. 538)	Sep. from trig. in adult.	Arises from trig. root.	No. r. op. prof., two ciliary rami.	
Class—Amphibia Order—Urodela				
Genus				
Spelerpes (Bowers '01)	Fused in adult.			
Ambylstoma (Coghill '02)	Fused with Gass. gang. and the ganglion of the anterior division of the Lat. VII root in adult.	Fused with trig. root.	r. op. prof. has 3 branches and performs function of R. op. and r. max. in frog tadpole. Passes below rectus superior and above rectus inferior and rectus internus.	

Amphiuma (Norris '08, p. 533)	Fused with gass. in adult.	Fused with trig. root.	r. op. prof. from anterior end of Gasserian 5 branches.
Order Anura			
Genus			
Rana (Strong '95)	Adult—Fused with trigeminus and Facial in 21 mm. embryo.		R. opthalmicus trigeminus
	Antero-ventral and middle portion of Gass. gang. particularly separate. No profundus described.		r. opthalmicus trig. supra-orbital but deep. From antero-ventral part of Trig. ganglion. Passes between rami of oculomotor.
(Landacre and Mc-Clellan '12, p. 463)	8 and 10 embryo, distinct but not detached from Gasserian.		r. opthalmicus seems at this time to come entirely from the profundus portion.
Class—Mammalia			
Guinea Pig (Chiarugi '94) (See Allis '97, p. 545)	Distinct opthalmic gang. but soon fuses with the trig. (unquestionably prof. ganglia of Amia (Allis '97, p.545).		r. opthalmicus.
Man (Streeter '08) (pp. 287-296)	Fused with Trig. in the adult, called semi-lunar ganglion (Wilder '09, p.456), 10 mm. embryo. No. prof. gang. described only a gang. semi-lunar.		10 mm. embryo. r. opthalmicus divides into frontal and naso-ciliary just dorsal to eye stalk.
(Ewart '90) (See Allis '97, p. 545)	5 mo. embryo vestiges of a profundus ganglion lying under cover of the inner portion of the Gasserian ganglion.		

In the Elasmobranchs the profundus ganglion is separate from the Gasserian and usually has a separate root even in the adult form. From this profundus ganglion arises the ventral ramus opthalmicus profundus which innervates the cutaneous tissues of the rostrum, and carries ciliary nerves and in one case noted (Acanthias) gives rise to the portio opthalmici profundi, which represents the dorsal branch of the primitive profundus nerve. (See Herrick '99, p. 364).

In the ganoids several different conditions exist. The Gasserian and profundus ganglia are usually separate in the adult, but a true ramus opthalmicus profundus is seldom present. According to Allis "a small, delicate, apparently degenerate nerve from the profundus ganglion" is in Amia the only remnant of the ramus opthalmicus profundus. There is a large portio opthalmicus profundus which fuses with the ramus opthalmicus superficialis V to form the supra-orbital trunk.

In teleosts the profundus ganglion is not isolated in the adult (Herrick '99) and no ramus opthalmicus profundus is described for any form so far as I know. Herrick homologizes cutaneous fibres which arise from the Gasserian ganglion and are fused with the radix longa from the ciliary ganglion with the ramus opthalmicus profundus of the Elasmobranchs. Allis takes the position that the ramus opthalmicus profundus is probably entirely wanting in Teleosts (p. 539) and that the ramus op sup V, probably contains the portio op. prof. The ramus opthalmicus profundus, whatever its relation to the muscles of eye (Allis '97, p. 536) always lies under the superior branch of the oculomotor and over the inferior branch of that nerve. In teleosts and ganoids a small branch of the trigeminus which is found dorsal to the oculomotor nerve must undergo a special development, i. e., become enlarged, as the rest of the profundus nerve disappears and become the portio opthalmicus profundus, which may be a separate nerve as in Amia, or be fused with the ramus opthalmicus superficialis V, as in Teleosts, according to Allis ('97, p. 539).

In the Amphibia the profundus ganglion is partially or entirely separate from the Gasserian in the embryo, but is always fused in the adult. In the adult Anura the trigeminal complex is also fused with the facial complex, but in the Urodeles the facial is separate. A ramus opthalmicus profundus is present and so named in almost every adult form of Urodele described (e. g. Coghill '12, Amblystoma).

Strong ('95) does not designate the opthalmic trunk arising from the Gasserian ganglion in Rana, as r. oph. profundus. He calls it the r. opthalmicus trigeminus. In discussing the problem of the profundus however, he seems (p. 193) to partially agree with Wilder ('92) who took the position that in Amphibia and the higher vertebrates the r. op. sup. V is fused with the r. op. profundus of the Elasmobranchs to form the r. op. trigeminus or supra-orbital trunk. Landacre ('12) finds that in the 8 mm. Rana embryo the r. opthalmicus comes almost entirely from the profundus portion of the ganglion, but in later stages derives some fibers from the Gasserian.

In higher terrestial vertebrates neither the r. opthalmicus profundus nor its ganglion are distinct in adult forms. A separate profundus ganglion has been found in the cat and the guinea pig embryos and Ewart ('90) found vestiges of it in the 5 mo. human embryo. The name ramus opthalmicus is the common term for the anterior trunk from the trigeminal or semi-lunar ganglion in higher vertebrates. The word profundus has dropped from the terminology of this complex and no hint is given that some fibers of this opthalmic trunk may have their origin in the profundus portion of the ganglion. The real morphology and origin of this nerve trunk is not known for the higher vertebrates and such forms as these would logically be the next to study after such a form as the Urodele where a r. opth. profundus is present and so named. The difficulty of obtaining a close series of embryos of the higher vertebrates makes the problem a serious one. The results of such studies would throw light on the question of what happens to the region innervated by a nerve when the ganglion on that nerve disappears or fuses with another. Such studies would also help to clear up the question of the fate of the profundus ganglion in phylogeny. It is evident from the summary given above that the urodeles occupy an intermediate position between types with a separate profundus ganglion and a distinct r. oph. prof. nerve in the adult and those types with neither profundus ganglion nor nerve in the adult; in that the urodeles have both structures separate in the embryo and in the adult have a distinct r. oph. prof. but fused Gasserian and profundus ganglia. The results of this study show that for Plethedon at least the ganglia of the adult are formed by an actual fusion of the profundus with the Gasserian without loss of cells by the profundus portion. This would not warrant the conclusion that the same process occurs in types where there is a loss of the r. oph. prof. nerve, but it throws an interesting light on the mode by which the process of reduction ending in loss of both profundus ganglion and nerve began in phylogeny.

LITERATURE CITED.

1897. **Allis, E. P. Jr.** The cranial muscles and cranial and first spinal nerves in Amia calva. Journ. Morph., vol. 12, no. 3.

1901. **Bowers, Mary A.** The peripheral distribution of the cranial nerves of Spelerpes bilineatus. Proc. Amer. Acad., vol. 36.

1902. **Coghill, G. E.** The cranial nerves of Amblystoma tigrinum. Jour. Comp. Neurol., vol. 12, pp. 205-289. Pl. 15-16.

1899. **Herrick, C. Judson.** The cranial and first spinal nerves of Menidia; a contribution upon the nerve components of the bony fishes. Jour. Comp. Neur., vol. 9, pp. 153-455.

1912. **Landacre, F. L.** The epibranchial placodes of Lepidosteus osseus and their relation to the cerebral ganglion. Jour. Comp. Neur., vol. 22, no. 1.

1913. **Landacre, F. L. and McLellan, Marie F.** The cerebral ganglia of the embryo of Rana pipiens. Jour. Comp. Neur., vol. 22, no. 5.

1908. **Norris, H. W.** The cranial nerves of Amphiuma means. Jour. Comp. Neur., vol. 15, no. 6.

1908. **Streeter, G. L.** The peripheral nervous system of the human embryo at the end of the first month. (10 mm.) Am. Jour. Anat., vol. VIII, no. 3.

1895. **Strong, Oliver S.** The cranial nerves of Amphibia. Jour. Morph., vol. 10, no. 1.

1892. **Wilder, H. H.** Die Nasengend von Menopoma alleghanense und Amphiuma tridactylum nebst Bemerkungen uber die Morphologie des R. opthelmicus profundus trigemini. Zool. Jahr. Abth. f. Anat. u. Ontog. Bd. 5, Heft 2.

ABBREVIATIONS.

Gal. E, Journ. Science, Dec.—(D)
Aud. G.—Auditory ganglion.
Aud. Ves.—Auditory vesicle.
B. B.—Base of the brain.
C. L.—Crystalline lens invagination.
Dien.—Diencephalon.
D. L. VII.—Dorso-lateral portion of the lateralis VII ganglion.
Ec.—Ectoderm.
Ec. Con.—Contact of the profundus ganglion with the lateral ectoderm.
En.—Endoderm.
En. D.—Endolymphatic duct.
Gass. G.—Gasserian ganglion.
Gen. G.—Geniculate ganglion.
Inf.—Infundibulum.
Med.—Medulla oblongata.
M. B.—Mid-brain.
Mes.—Mesenchyme.
N. C.—Nasal capsule.
O. V.—Optic vesicle.
Pal. VII.—Palatine branch of VII.
Ph.—Pharynx.
Ph. P. I.—First visceral pouch of the pharynx.
Pl.—A supra-orbital placode of the lateral line series.
Prof. G.—Profundus ganglion.
R. aveolaris VII.—Ramus aveolaris VII.
R. Bucc. VII.—Ramus buccalis VII.
R. Max. V.—Ramus maxillaris V.
R. op. Prof. V.—Ramus opthalmicus profundus V.
R. op. Sup. VII.—Ramus superficialis VII.
Rt. Gass. G.—Root of the Gasserian ganglion.
Rt. Prof. G.—Root of the profundus ganglion.
Tel.—Telencephalon.
V. L. VII.—Ventro-lateral portion of the lateralis VII ganglion.

Explanation of Figures.

All sections were cut 10 micra thick and all reconstructions and drawings were made from transverse sections. Flat reconstructions at 150 diam., detailed drawings at 520 diam. and outlines at 80 diam. were made with a camera lucida. All figures were reduced to one-third and the magnification after reduction is given after the description of each figure. Figures 1 to 6 inclusive are from the same embryo. (Plethedon gl. stage m. 9 mm.) from which the flat reconstruction Fig. 30 was made.

Plate II.

Figure 1 is a detailed drawing of the profundus near the level of the middle of the crystalline lens and seven sections posterior to the anterior end of the profundus. (See Fig. 2). Large yolk granules appear as light areas in the mesenchyme. The pigmented cytoplasm of the ganglion is shown by darker, solid stippling. Sec. 62 × 175.

Figure 2 is an outline of the section of which a portion is detailed in Fig. 1. ×27.

Figure 3 is an outline of a section at the level of the optic stalks and just posterior to the crystalline lens. Sec. 69. × 27.

Figure 4 is a detailed drawing of the trigeminal complex at the level of the root. (See Fig. 5). The fibrous root of the Gasserian ganglion is shown (Rt. Gass. G.). A profundus root cannot be distinguished in the figure nor identified in the section from which it was drawn. Sec. 90. × 175.

Figure 5 is an outline of the section of which a portion is detailed in Fig. 4. Sec. 90. ×27.

Figure 6 is an outline of a section through the main portion of the Gasserian ganglion half way between its root and its posterior end. The D. L. VII is shown lateral to the Gasserian ganglion which shows the characteristic forking over the first visceral pouch of the pharynx. (Ph. P. 1). Sec. 95. ×27.

Figures 7 to 15, inclusive, are all from the same embryo (Plethedon gl. Stage G. 7 mm.) from which the flat reconstruction of Fig. 31 was made.

Figure 7 is a detailed drawing of the profundus ganglion at the level of Fig. 8, six sections posterior to the anterior end. The irregular outline of the ganglion is shown and its position relative to a supra-orbital placode of the lateral line series (P1). The placode appears as a thickening of the ectoderm. The nuclei in the inner layer, containing a mitotic figure, are seen to have a radial arrangement. Sec. 52. ×175.

Figure 8 is an outline of the section of which a portion is detailed in Fig. 7. × 27.

Figure 9 is an outline of the section of which a portion is detailed in Figure 10. This section is at the level of the open optic stalks and the middle of the crystalline lens. Sec. 68. ×27.

Fig. 1

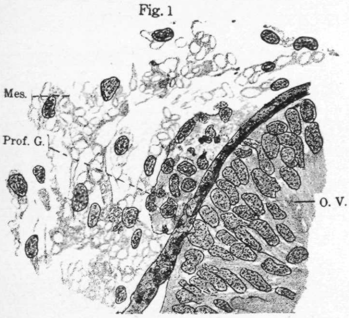


Fig. 2

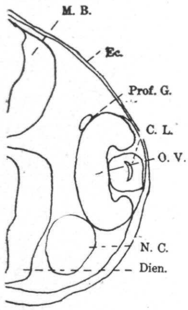


Fig. 3

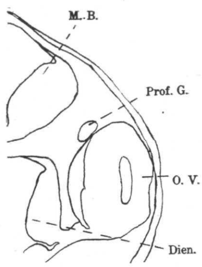


Fig. 4

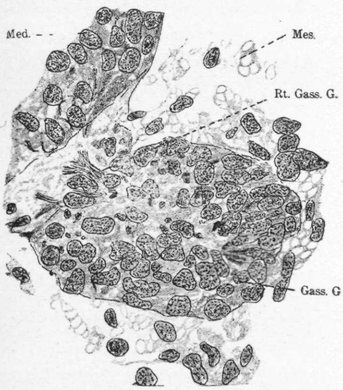


Fig. 5

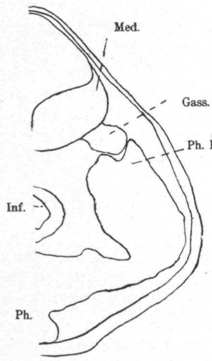


Fig. 6

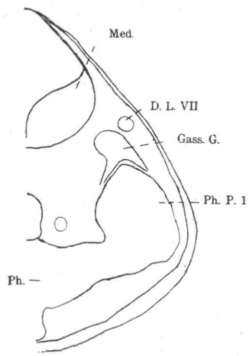


Fig. 7

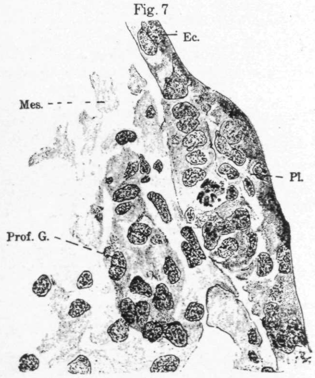


Fig. 8

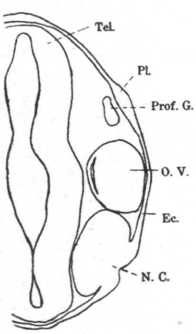
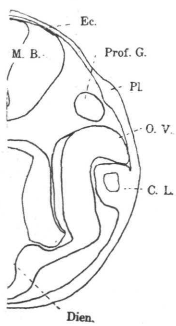


Fig. 9



Katherine Okey.

PLATE III.

Figure 10 is a detailed drawing of the profundus at the level of Figure 9. The definite boundaries and compactness of the ganglion stand out clearly in the figure. This figure also illustrates the relation of the ganglion to a supra-orbital placode (Pl), the nuclei of which show a radical arrangement. Sec.68 ×175.

Figure 11 is a detailed drawing of the profundus at the level of its root in the medulla. The root is cellular, as the figure shows and is at this level separate from the root of the Gasserian. Sec. 86. ×175.

Figure 12 is an outline of the section of which a portion is detailed in Fig. 11. Sec. 86. × 27.

Figure 13 is a detailed drawing of the trigeminal complex seven sections posterior to the beginning of the root of the profundus. This figure is drawn from the left side of the section because it showed the double root more clearly than the right side. Sec. 93. × 175.

Figure 14 is an outline of the section of which a portion is detailed in Fig. 13. Sec. 93. × 27.

Figure 15 is a detailed drawing of a portion of the Gasserian ganglion at the level of Fig. 16. Only the part over the gill pouch is detailed. The close relation of the ganglion to a lat. line placode (pl.) is shown and also its contact with the endoderm (en) of the gill pouch. Sec. 94. × 175.

Figure 16 is an outline of the section of which a portion is detailed in Fig. 15. Sec. 94. ×27.

Figures 17 to 27, inclusive, are from the same embryo (Plethedon gl. Stage B, 6 mm.) from which the first reconstruction Fig. 32 was made.

Figure 17 is a detailed drawing of the profundus ganglion with the ectoderm (ec) is shown and also the irregular outlines of the ganglion. Sec. 45. × 175.

Fig. 10

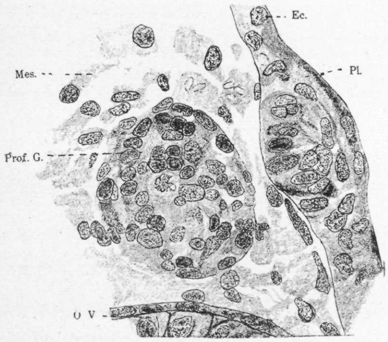


Fig. 12

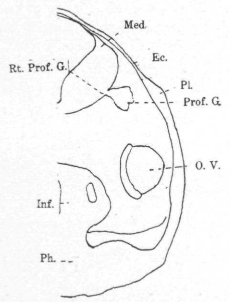


Fig. 14

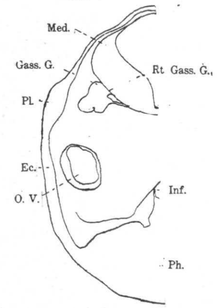


Fig. 11

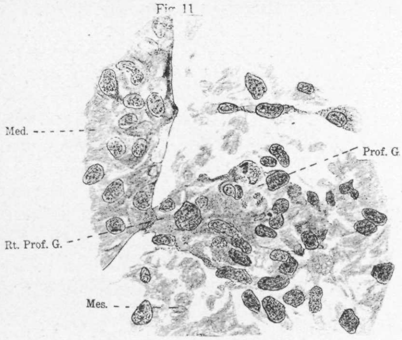


Fig. 13

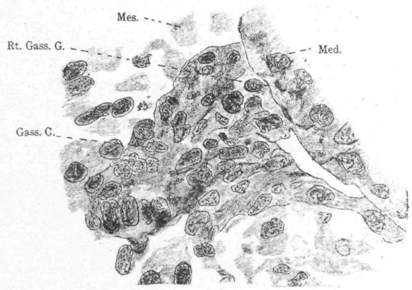


Fig. 15

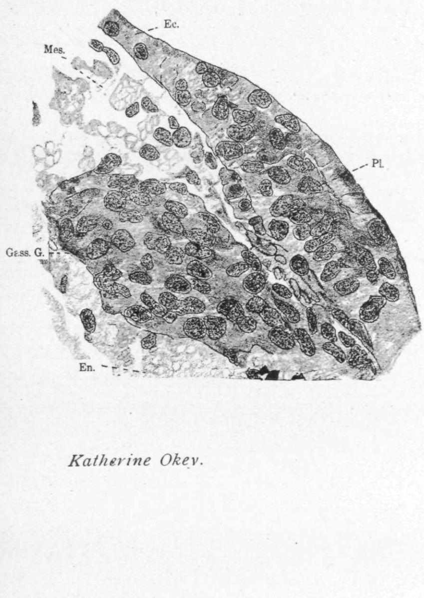


Fig. 16

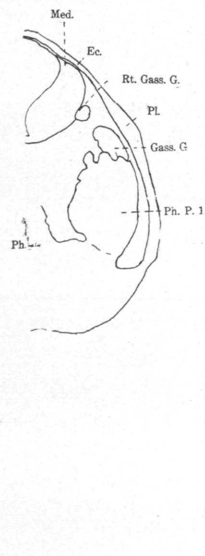


Fig. 17

Katherine Okey.

PLATE IV.

Figure 18 is an outline of the section of which a portion is detailed in Fig. 17. This section is three or four sections posterior to the anterior end of the profundus. Sec. 45. × 27.

Figure 19 is a detailed drawing of the profundus at the level of Figure 20. The ventro-lateral attachment of the profundus to the lateral ectoderm is shown. The loose structure of the ganglion and its irregular outline are also shown. Sec. 56. × 175.

Figure 20 is an outline of the section of which a portion is detailed in Fig. 19. Sec. 56. × 27.

Figure 21 shows in detail the extreme posterior end of the profundus ganglion slightly anterior to the level of the evagination of the optic stalks. The ganglion appears very small in this figure. Large yolk granules appear as light areas in the surrounding mesenchyme. (See Fig. 22). Sec. 67. × 175.

Figure 22 is an outline of the section of which a portion is shown in detail in Fig. 21. Sec. 67. × 27.

Figure 23 shows in detail the extreme anterior end of the Gasserion ganglion which appears as a small, darkly stippled mass. The level is that of Fig. 24. The anterior end of a placode is shown (Pl). Sec. 76 . × 175.

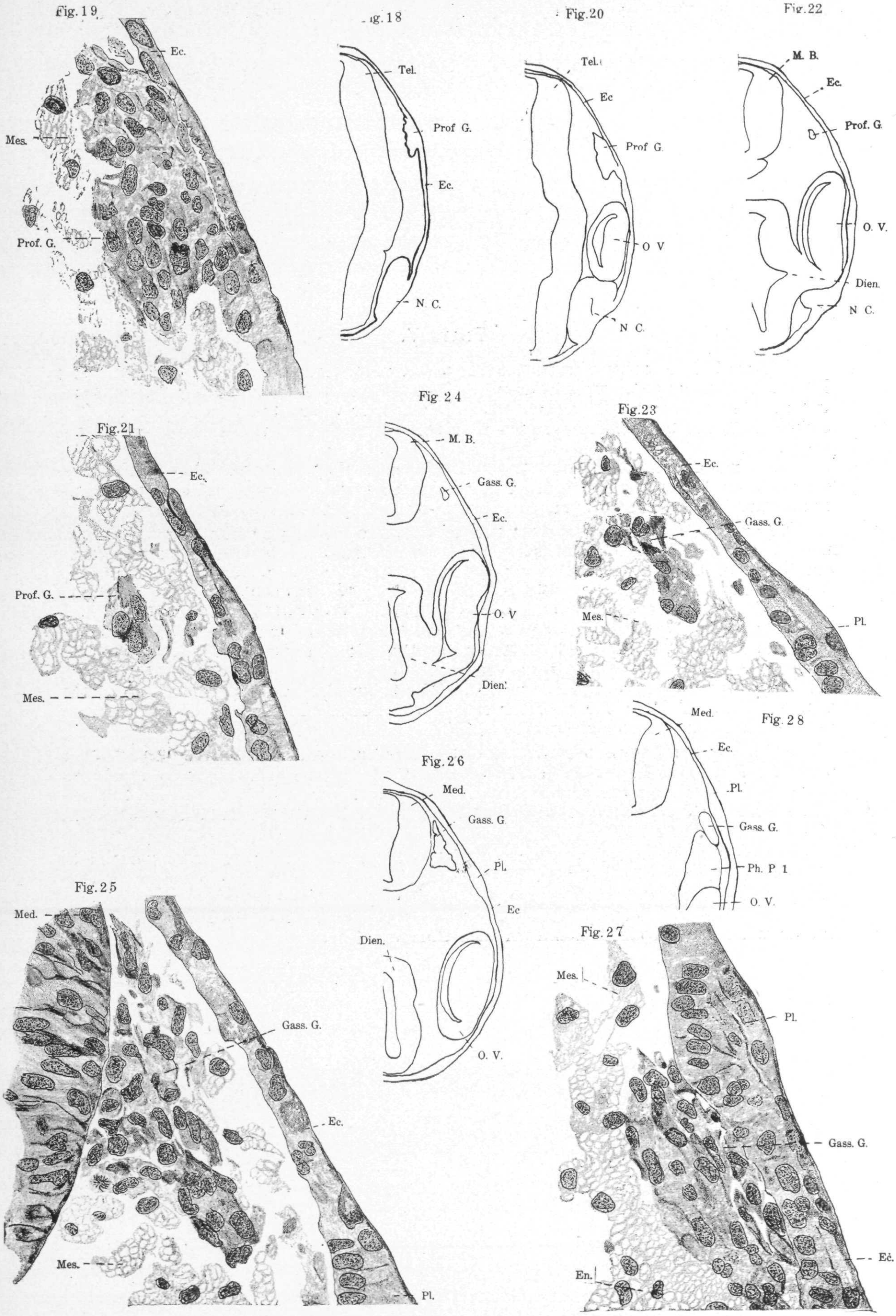
Figure 24 is an outline of the section of which a portion is shown in detail in Fig. 23. Sec. 76. × 27.

Figure 25 shows in detail the characteristic condition of the Gasserian ganglion near its middle part. The relation to the medulla is shown. No root, either cellular or fibrous, appears. Sec. 85. × 175.

Figure 26 is an outline of the section of which a portion is detailed in Fig. 25. Sec. 85. × 27.

Figure 27 shows in detail the posterior part of the Gasserian ganglion. It lies in contact with the first visceral pouch (Ph. p. 1, Fig. 28) and near a placode of the lateral line series (Pl). × 175.

Figure 28 is an outline of the section of which a portion is detailed in Fig. 27. Sec. 94. × 27.



Katherine Okey.

PLATE V.

Figure 29. A copy of a portion of a flat reconstruction by W. J. Kostir of a Plethedon embryo 11.5 mm. in length. The scale at the top of the figure indicates the number of sections 10 micra in thickness over which the plot extends. The figures indicate the numbers of the sections, counted from the anterior end of the body.

This reconstruction shows the most fused embryonic condition of the trigeminal complex so far studied. The profundus portion is not distinct; the nerve trunks are formed and the ganglion is over-lapped by the D. L. VII. × 66.

Figure 30 is a flat reconstruction of the Gasserian, profundus and a part of the D. L. VII of Plethedon gl. stage M, 9 mm. in length. This shows a well fused condition of the Trigeminal complex and a single root, which is indicated by dotted lines (Rt. Gass. G.). An outline of a longitudinal section of the head was made on coordinate paper with a camera lucida. This outline was used as a horizontal axis and guide in making the reconstructions of the transverse sections. The same method was used for the reconstructions shown in Figs. 31 and 32. The scale at the top of the figure indicates the number of sections 10 micra in thickness over which the plot extends. The figures indicate the numbers of the sections counted from the anterior end of the body. The levels of the sections detailed in Figures 1 to 6 are given. × 50.

Figure 31 is a flat reconstruction of the Gasserian and profundus ganglia and a part of D. L. VII of Plethedon gl. stage G., 7 mm. in length. The roots of profundus and Gasserian are separate at this stage. A dotted line indicates the line of contact of the profundus and Gasserian posterior to the root of profundus. × 50.

Figure 32 is a flat reconstruction of the Gasserian and profundus ganglia of Plethedon gl. stage B., 6 mm. in length. The ganglia have no roots at this stage. This shows the unfused condition of the profundus and the Gasserian and the number of sections by which they are separated. The contact of the profundus with the ectoderm is shown (Ec. Con.). × 50.

Fig. 29

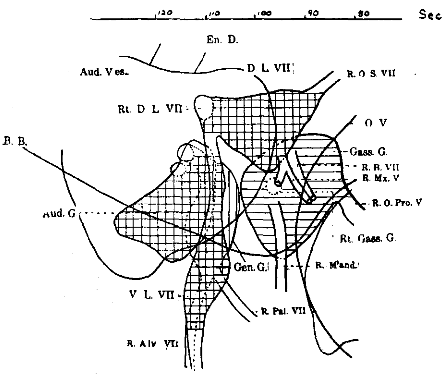


Fig. 30

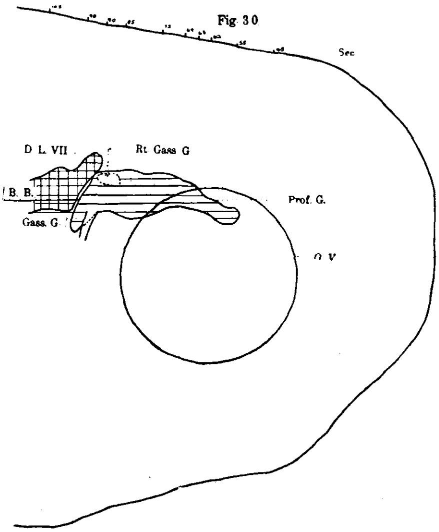


Fig. 31

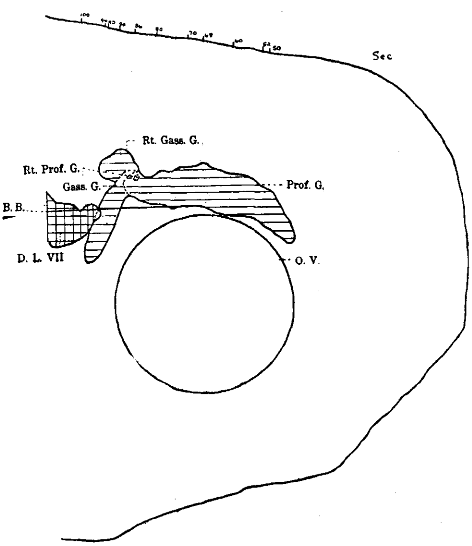
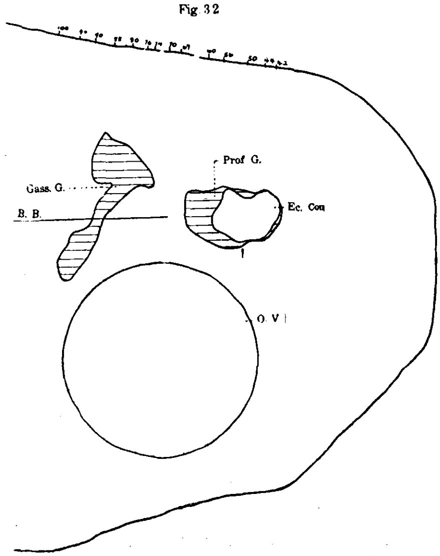


Fig. 32



Katherine Okey.